What controls the floristic diversity of a National Park? Species turnover as a common currency for quantifying diversity patterns within the Great Smoky Mountains and among 23 National Parks

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A major deterrent to understanding what controls diversity over large regions is the lack of a robust, systematic measure of how environmental factors control species turnover in space. Moreover, vegetation and environmental data have rarely been available with the extent or detail necessary to examine floristic patterns along broad environmental gradients of many types (climate, topography, soil). We have developed a technique that explicitly calculates the rate of species accumulation along environmental gradients. For the first time, we can determine which environmental factors impose the greatest constraints on species turnover through space, and how species accumulation rates for a particular factor vary among regions. We will conduct a detailed analysis of species turnover along important gradients in Great Smoky Mountains National Park, after sampling under-represented portions of the park's vegetation. We will then compare species turnover rates along particular topographical and climatological gradients at 23 NPS sites, using newly available vegetation data from the NPS Vegetation Mapping project and a high-resolution climate database. In addition to providing groundbreaking information on how floristic diversity is controlled by environment, our project will greatly inform how diversity is to be sampled over the landscape.

Research Question and Introduction

What controls the floristic diversity of a National Park? Beyond the influences of area, disturbance, and dispersal factors, the range and number of environmental gradients and the rate at which species turn over along those gradients stand out as crucial factors. Although plant ecologists have a general understanding of how diversity changes along environmental gradients at large scales (e.g., control over physiognomy by annual precipitation and temperature), and by particular factors at particular locations (e.g., elevation and topographic gradients, salinity in coastal marshes), actual rates of species turnover with respect to environmental gradients have never been systematically determined. As a result, basic understanding of controls over regional diversity remains elusive: Which environmental gradients most influence species turnover? Is the turnover rate for a particular environmental factor consistent among regions?

What if rates of species turnover along environmental gradients could be quantified? Turnover rates along different gradients could be compared, allowing examination of which factors exert the most control over diversity through space (is elevation or soil calcium more important, and at which scales?). With knowledge of compositional history of particular regions, turnover rates due to particular factors could be compared among regions to determine the extent to which adaptation versus historical factors control regional diversity (is turnover higher along a particular gradient in more historically stable regions?). More practically, turnover rates could be used as an essential tool for taxonomic inventory efforts: How many plots are needed to adequately sample regional biodiversity, and how should they be positioned on the landscape?

Given this potential utility, why has the quantification of species turnover rates with respect to environmental variation never been performed? Much of the reason is methodological—until recently, vegetation data were available only from relatively small geographic extents and usually were not accompanied by detailed environmental data but rather complex and easily measured topographic variables (elevation, exposure). Soil properties were almost never measured over large extents, and climate variables were not available at high enough resolutions. The nature of vegetation and environmental data is changing, however, due to the recent availability of large amounts of plot data covering very large extents. Remote sensing and climate modeling are producing environmental and climate data at high resolutions.

With this recent influx of large-extent, high-resolution data, it is now possible to ask large-scale, multi-regional questions about controls over floristic diversity, and such studies have the potential to fundamentally change our understanding of how diversity is distributed on the landscape. All that is needed are analytical techniques appropriate for these data, such that controls over diversity in one region can be compared to those in another. The way to do this is to create a common currency describing the distribution of diversity over the landscape in relation to important environmental gradients—similar to recent calculations of beta-diversity among different regions (Nekola and White 1999, Condit et al. 2002). This would make the study of vegetation description and analysis—a largely subjective endeavor plagued by a panoply of methods—a systematic search for the controls of regional floristic diversity.

One of the great natural laboratories for the study of vegetation and diversity has been Great Smoky Mountains National Park (GSMNP). Classic studies such as that by Whittaker (1956) give the impression that the main environmental gradients controlling floristic diversity are well understood. This is far from the case—there are no available estimates of how certain gradients influence rates of species turnover, only a few main gradients have been investigated (elevation, exposure, disturbance), and there remains no basis for extrapolating what is known about species turnover along these gradients to other regions. Not enough information is available to predict how floristic diversity is distributed along gradients within GMSNP, to say nothing about how this information could be used to inform studies of how floristic diversity is controlled in elsewhere in the world.

Under the guidance of Peter White, a leading expert on the vegetation of GSMNP, I propose a three-year project focused on constructing a common currency for measuring species turnover along environmental gradients, and applying this method to the vegetation of GSMNP and that of other National Parks from many different regions. I am motivated by two central questions. First, what are the rates of species turnover along the major environmental gradients of GSMNP—that is, what are the major controls over GSMNP floristic diversity? Resolving this will require refinement and application of a newly developed analysis, and—critically—the sampling of under-represented vegetation and environmental variables in GSMNP. Second, how do these turnover rates compare to those calculated from other parks—are certain factors always important, regardless of spatial extent or region? Can turnover patterns from different regions be used to determine the extent to which floristic diversity is controlled by adaptation to environmental factors versus historical factors? This multi-park floristic comparison is facilitated by the recent availability of vegetation data from the USGS-NPS Vegetation Mapping project from 23 NPS sites and a new small-resolution climate database of the contiguous U.S.

Research background

Identifying relationships between vegetation and the environment is one of the oldest pursuits in all of ecology (Humbolt and Bonplan 1805, Warming 1909, Whittaker 1956); it is thus surprising that it remains one of ecology's less resolved endeavors. A major problem is that there is no standard currency for describing species turnover along gradients; researchers have been content describing the main environmental correlates of compositional variation for particular locales, using very different, often subjective multivariate methods (Kent and Coker 1992, McCune et al. 2002). Indeed, only recently has large-scale species turnover been studied on a quantitative basis (Nekola and White 1999, Hubbell 2001, Condit et al. 2002), and none of these studies have explicitly measured turnover in relation to environmental gradients.

Identifying factors that influence vegetation distribution and species diversity within GSMNP has been a common research theme for many decades (e.g., Cain 1935, Whittaker 1956, Bratton 1975, Golden 1981, Harmon et al. 1984, Callaway et al. 1987, Busing et al. 1993, White et al. 2001). GSMNP is an ideal location for vegetation studies due to its size, relative lack of human disturbance, and its great diversity of habitats and important environmental gradients. Its size and habitat diversity largely account for the fact that the vegetation is still significantly under-sampled (White and Busing 1993). Coupled with new techniques for the analysis of species turnover, a more complete description of the vegetation of GSMNP has great potential for understanding of the underlying causes of regional floristic diversity.

Research methods and timetable

Three separate research components will compose our three-year project: 1) two summer field seasons of vegetation and environment sampling in GSMNP; 2) collection and assimilation of vegetation and environment data from 23 NPS sites; and 3) use of these data in a newly developed analysis that quantifies the degree to which each environmental factor influences species turnover, including a detailed analysis within GSMNP followed by a multi-park comparison of turnover rates among particular gradients.

1. *Sampling under-represented vegetation and environmental gradients in GSMNP.*

In the 1930s, a thorough and systematic sampling of tree species in about 1500 plots was performed throughout GSMNP. Since then, vegetation plots with available plant composition data have not been well distributed across the geography or major environmental gradients of GSMNP; rather, their distribution is highly clustered and reflects particular projects that involved often small areas. The North Carolina side of the park and the eastern portion in general are poorly represented in the current data, and virtually no soil data exist. Available data and portions of the park covered up to 1993 are described in detail by White and Busing (1993).

In collaboration with park personnel and other vegetation researchers, we will conduct a thorough inventory of the available vegetation data from GSMNP to supplement the White and Busing (1993) study, discuss which portions of the presumed important environmental gradients and geographic areas are currently represented, and then delineate the appropriate regions in need of sampling. In two field seasons of eight weeks each for a team of four, we expect to sample on average 1.5 plots per day for a total of 80 days, or 120 total plots.

Vegetation plots will be sampled using the protocol of the Carolina Vegetation Survey, described fully in Peet et al. 1998. Briefly, this protocol includes a sampling design that records all vascular plant species by cover class in 10 x 10 m "modules" that can be combined to form 20 x 50 m (0.1 ha) contiguous samples. Modules may be intensively sampled in non-independent sets of nested quadrats to address the effects of sample grain on vegetation pattern. Soil samples will be taken from both A and B horizons within each sampling unit, frozen for storage and then sent off for laboratory nutrient and texture analysis. Various environmental and geographic descriptors will also be recorded, including soil depth, approximate hydrologic regime, topographic position, UTM coordinates, and landform type. Two field workers will assist me in the field for 8 weeks distributed in May, June, July, and August 2004 and 2005. After each field season, data will be entered into the established database of the Carolina Vegetation Survey housed in the laboratory of Robert Peet and Peter White at UNC-Chapel Hill.

2. *Assimilation of vegetation and environment data for 23 NPS sites.*

Comparisons of our analysis of species turnover in GMSNP to those for other National Park sites requires available vegetation and environment databases from other parks that we will not be sampling. For this purpose, we will be using two major sources of freely available vegetation and environment data (described below): vegetation field data from the USGS-NPS Vegetation Mapping Program in 23 NPS sites; and an integrated weather station and model-based climate database of the contiguous U.S. These data will be assembled into an MS Access database of several tables (data layers), including vegetation composition, various plot-based variables (geocoordinates, elevation, etc.), climate variables, and soil data when available.

The National Park Vegetation Mapping Program Data includes field vegetation data from NPS sites all over the country for the purposes of producing vegetation maps describing the distribution of vegetation types (from the National Vegetation Classification) along major environmental gradients. These data are being collected with a common method (TNC and ESRI 1994) and are currently available from 23 parks in 19 states, representing 15 Bailey Ecoregions (details online[1]). As a whole these data contain 2897 vegetation samples, and only a few of the 23 parks are

[1] http://biology.usgs.gov/npsveg/

represented by less than 50 plots; some parks are represented by several hundred (Yosemite = 607). Furthermore, several topographic and environmental descriptors are available for most vegetation plots, including landscape variables (slope, aspect, elevation) and geocoordinates to link plots to other datasets. These data are for public use and web-accessible.

The Daymet Climatological Database includes all major climate summary variables interpolated from thousands of weather stations to produce 1 km^2 spatial resolution data gridded across the entire contiguous U.S. Each vegetation sample in the U.S. can now be assigned climate information at a 1 km^2 resolution; plots in separate grids of this database are thus assigned semi-independent climate values, including critical variables for predicting plant species adaptation and spatial turnover (temperature, precipitation, frost days per year, radiation, humidity, etc.; full details found online[2]; see also Thornton et al. 1997). All data are for public use and freely web-accessible.

3. *Analysis of environmental controls over species turnover, within GSMNP and among parks.*

Environmental factors strongly influence how species are distributed over the landscape. Species turnover (the addition and loss of species through space) and the rate at which species accumulate over environmental gradients are two interrelated ways of measuring this landscape component of diversity. We have been developing a technique that is explicitly designed for robustly measuring the rate of species accumulation along an axis of variation of an environmental factor. This technique is particularly appropriate for vegetation data of large spatial extent (GSMNP and beyond) but relatively small sample resolution (ha and below), as it does not concern compositional similarity and thus whether plots share species. In short, we construct species accumulation curves by aggregating plots according to spatial or environmental "proximity"; i.e., species accumulate along axes of environmental variation as they would accumulate over time or space. We assume that initial slower rates of accumulation along certain gradients demonstrate greater constraints on diversity by those particular environmental factors. Because we use the same species pool and plot distribution for the calculation of this rate for each environmental factor, we are able to compare initial species accumulation rates for factors that are measured in very different units (rainfall, nutrient concentration, frost days, etc.).

Furthermore, a common currency can be calculated that describes the rate of species accumulation along a particular gradient at a particular spatial resolution. For example, for a given set of plots, we can make the statement, "Species accumulate at a rate of 5 species per 0.1 ha per 100 m elevation." This statement is an estimate of species turnover along a particular gradient that can then be compared among regions. We will employ this technique for GSMNP vegetation data using all available environmental variables, including Daymet climate data, complex gradients such as elevation and exposure, and soil nutrient and texture data as it becomes available. Concurrently, we will perform the same analysis using NPS Vegetation Mapping data coupled to climate data, and any other available plot data associated with these plots (elevation, slope, aspect, etc.). Our central aims are to: 1) rank the principal environmental factors that

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[2] http://www.daymet.org

most constrain species accumulation at GSMNP; and 2) determine whether rates of species accumulation along certain environmental (particularly climate) gradients are similar in different, widely separated parks. Our use of this technique on preliminary vegetation data of North and South Carolina generally conform closely to intuitive expectations of which variables are most correlated with species turnover.

<u>Timetable</u>

August 03	Begin compilation of existing vegetation data of GSMNP
	Begin assimilation of NPS vegetation mapping data and climate database
Oct 03 – Apr 04	Identify sampling locations in GSMNP
	Preliminary analyses of species turnover with NPS veg mapping data
May – Aug 04	Field season 1: vegetation and environment sampling in GSMNP
Sept 04 – Apr 05	Data entry; soil analysis batch 1
	Review GSMNP sampling scheme; identify more sampling locations
	Analysis: species turnover with NPS vegetation and climate data
May – Aug 05	Field season 2: vegetation and environment sampling in GSMNP
Sept 05 – July 06	Data entry; soil analysis batch 2
	Final analyses using all available GSMNP data and all NPS sites

Significance of Research

Quantifying the influences of particular environmental factors on floristic spatial turnover will be a critically important way of describing and predicting floristic diversity for a given region. From a conservation standpoint, knowledge of the rates of species turnover along important environmental gradients allows predictions of regional diversity if environmental distributions are known for a given area. This knowledge would also suggest sampling locations most likely to contain new species, and thus is an important guide for floristic inventory efforts (as well as other taxonomic groups). The All Taxa Biodiversity Inventory at GSMNP (Science Committee co-chaired by Peter White) calls for a systematic park-wide survey of new plots. Our project will help inform how this should done, supplying critical information on plot distribution.

The significance of our research is also manifest in its contributions to basic research in the controls of biodiversity. By quantifying rates of species turnover in relation to environmental factors explicitly for the purposes of cross-regional comparisons, we address a dire need for synthetic, cross-site ecological studies. For example, our analysis of species turnover in different regions with different known histories will greatly improve knowledge of processes related to adaptation versus historical factors, one of the principal issues in biogeography. Finally, information on rates on species turnover in relation to climate factors is critical to the further development of accurate predictions of the influence of climate and other environmental change on the distributions of species and vegetation. Such information will help NPS and other management agencies establish priority areas for species conservation.

Budget (as of Aug 28, 2003)

Year 1

Research stipend	$36,000
Computer support	$3,000
Field assistants (2)	$6,400
Field equipment	$1,800
Travel	$2,800
TOTAL, Year 1	$50,000

Year 2

Research stipend	$36,000
Field assistants (2)	$6,400
Soils	$4,000
Field equipment	$800
Travel	$2,800
TOTAL, Year 2	$50,000

Year 3

Research stipend	$36,000
Research assistant	$8,000
Soils	$4,000
Scientific meetings	$2,000
TOTAL, Year 3	$50,000

Budget Justification

Research stipend. Includes fringe benefits.

Computer support. One high-end desktop system required for the analysis of two large databases (NPS vegetation mapping data, Daymet climate data), in addition to sampled vegetation data from GSMNP.

Field assistants. Two field assistants for eight weeks in May, June, July, and August at the end of the first two years (2004, 2005). Before tax pay is $10/hr, for 8 hr/d, 5 d/wk, 8 weeks = $3200 per person per season, or $6400 total in field assistant pay per year.

Field equipment. Lab of Peter White at host institution provides main sampling equipment, including GPS units, meter and dbh tapes, clinometers, etc. We will spread out $2600 over two field seasons to cover the costs of disposable supplies (paper and plastic bags for soil samples, data sheets, etc.) and worn or broken equipment.

Travel. Round-trip car travel from Chapel Hill to GSMNP is about 600 miles; at $.33/mile this is $200 per round trip in gas expense. Five to eight round tips per field season is $1000-$1600. Shuttling to field sites will amount to 100-150 miles per week, for up to $400 additional gas expense per field season. Although we anticipate free camping accommodations in GSMNP, occasional motel stays may be necessary in certain areas, requiring an additional $800 per season. We therefore believe $2800 is a reasonable per-season travel allotment.

Soils. Represents an estimate of 60 plots per season, 6 samples per plot at $10 per sample plus shipping costs for a full soil nutrient and texture analyses performed by Brookside Laboratories (Ohio), a soil laboratory commonly used by the Carolina Vegetation Survey.

Research assistant. Primarily for the final year, involving data entry and preparation of soil samples for lab analysis. Includes salary and fringe benefits for one university semester.

Scientific meeting. Airfare, registration, and room and board for two standard 5-day scientific meetings.

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